

Subtribes of Principally North American Genera of Cichorieae (Compositae)

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ABSTRACT. A new subtribal classification for principally North American genera of Cichorieae allows for a practical taxonomy that reflects recent phylogenetic hypotheses. We propose the new subtribes Lygodesmiinae (for *Chaetadelpha*, *Lygodesmia* sensu Tomb, and *Shinnersoseris*), Pinaropappinae (for *Marshalljohnstonia* and *Pinaropappus*), Pyrrhopappinae (for *Picrosia* and *Pyrrhopappus*), and three monogeneric subtribes (Glyptopleurinae (*Glyptopleura*), Krigiinae (*Krigia*), and Phalacroseridinae (*Phalacroseris*)) for taxa previously treated in Malacothricinae, Microseridinae, and Stephanomeriinae. We recognize novel circumscriptions for Malacothricinae (*Anisocoma*, *Atrichoseris*, *Calycoseris*, and *Malacothrix*), Microseridinae (*Agoseris*, *Microseris*, *Nothocalais*, *Stebbinsoseris*, and *Uropappus*), and Stephanomeriinae (*Munzothamnus*, *Pleiacanthus*, *Prenanthes*, *Rafinesquia*, and *Stephanomeria*). The revised classification provides a more precise taxonomic representation of relationships among genera, insofar as robust resolution of monophyletic groups currently allows.

Key words: Cichorieae, Lactuceae, Malacothricinae, Microseridinae, Stephanomeriinae, subtribes, taxonomy.

Phylogenetic analyses of 18S–26S nuclear rDNA external and internal transcribed spacer sequences (Lee et al., 2002, 2003) and chloroplast DNA restriction sites (Jansen et al., 1991; Whitton et al., 1995) yielded evidence for new hypotheses of relationship among all genera of Cichorieae (Lactuceae) that have natural centers of diversity in North America (plus *Picrosia*, endemic to South America). On the basis of molecular findings, Lee et al. (2003) concluded that taxa previously treated in subtribes Malacothricinae, Microseridinae, and Stephanomeriinae (e.g., Stebbins, 1953; Bremer, 1993, 1994) or in Jeffrey's (1966) "Microseris subgroup" and "Stephanomeria subgroup" represent a single major radiation, with a large western North Amer-

ican component. As previously treated, each of those subtribes and subgroups is evidently paraphyletic or polyphyletic. To better reflect phylogenetic relationships, we propose revised circumscriptions for Malacothricinae, Microseridinae, and Stephanomeriinae and recognize six new subtribes.

Malacothricinae K. Bremer, Novon 3: 329. 1993.

TYPE: *Malacothrix* DC.

Annual or perennial herbs. Leaf blades linear, elliptic, lanceolate, oblanceolate, obovate, or spatulate; margins entire, denticulate, lobed, or pinnatifid. Capitulescences corymbiform or capitula borne singly (peduncles scapiform). Receptacles not paleate, bristly or not bristly. Involucres cylindrical to obconic or campanulate. Phyllaries in 3 to 6 series, unequal (1 or 2 subequal series in *Atrichoseris*). Florets 15 to 250 per capitulum. Corollas yellow or white (often with abaxial reddish stripes). Cypselae columnar to fusiform, 5- to 15-ribbed or -veined (5 usually prominent), beaked (*Calycoseris*) or not beaked. Pappi 0 (*Atrichoseris*) or of 15 to 40 subequal, barbellate or, rarely, plumose (*Anisocoma*), persistent or often (all or mostly) caducous or fragile bristles and sometimes an outer crown of minute teeth. Pollen echinate (Tomb et al., 1974). Chromosome number $2n = 14, 18, 20$.

Included genera: *Anisocoma* Torrey & A. Gray, *Atrichoseris* A. Gray, *Calycoseris* A. Gray, *Malacothrix* DC.

Microseridinae Stebbins ex Solbrig, Taxon 12: 234. 1963. TYPE: *Microseris* D. Don.

Annual, biennial, or perennial herbs. Leaf blades linear, oblong, lanceolate, oblanceolate, or spatulate; margins entire, denticulate, sinuate, lobed, or pinnatifid. Capitulescences branched or, often, capitula borne singly (peduncles scapiform). Receptacles not paleate, not bristly. Involucres subcylindrical to obconic or campanulate. Phyllaries in

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2+ series, subequal or unequal, the outer sometimes forming calyculi. Florets 5 to 300+. Corollas yellow, orange, or white (sometimes with abaxial reddish stripes). Cypselae columnar or fusiform, \pm 10-ribbed, beaked (*Agoseris*) or not. Pappi of (0)2 to 90 equal or unequal, smooth to barbellate (rarely plumose) bristles or bristle-tipped scales, persistent or caducous. Pollen echinolophate (Feuer & Tomb, 1977). Chromosome number $2n = 18, 27$ (triploid), or 36.

Included genera: *Agoseris* Rafinesque, *Microseris* D. Don, *Nothocalais* (A. Gray) Greene, *Stebbinsoseris* K. L. Chambers, *Uropappus* Nuttall.

Stephanomeriinae Stebbins ex Solbrig, Taxon 12: 235. 1963. TYPE: *Stephanomeria* Nuttall.

Annual or perennial herbs, or shrubs. Leaf blades linear, oblong, lanceolate, oblanceolate, ovate, or scale-like; margins entire, sinuate-dentate, lobed, or pinnatifid. Capitulescences corymbiform to thyrsoid-paniculiform. Receptacles not paleate, not bristly. Involucres narrowly cylindrical or obconic. Phyllaries usually in 2 series, unequal (outer forming calyculi), sometimes graduated (*Stephanomeria cichoriacea*). Florets 3 to 15 (to 30 in *Rafinesquia*) per capitulum. Corollas pink, purple, or white. Cypselae clavate, columnar, or fusiform, smooth, sometimes grooved or ≤ 5 -ribbed, beaked (*Rafinesquia*) or not. Pappi of 5 to 20+ equal or unequal (*Prenanthes*), plumose (*Rafinesquia*, *Stephanomeria*), or barbellate, persistent, or deciduous (*Munzothamnus*) bristles. Pollen echinate (Tomb et al., 1974). Chromosome number $2n = 14$ (*Prenanthes*), 16, 24 (triploid), or 32.

Included genera: *Munzothamnus* P. H. Raven, *Pleiacanthus* Rydberg, *Prenanthes* Rydberg, *Rafinesquia* Nuttall, *Stephanomeria* Nuttall.

Glyptopleurinae Joongku Lee & B. G. Baldwin, subtribus nov. TYPE: *Glyptopleura* D. C. Eaton.

Herbae annuae. Laminae foliorum spatulatae vel oblongae, profunde lobatae vel pinnatifidae; margines albi, scariosi, dentati vel setoso-ciliati. Capitula portata singulatim vel capitulescentiae parce ramosae. Receptacula epaleata, non setosa. Involucra cylindracea vel urceolata, ad bases bracteae spatulatis marginibus albis, scariosis, dentatis. Phyllaria 2-seriata, \pm aequalia. Flosculi 7–16. Corollae cremeae vel luteolae (in sicco subroseae). Cypselae clavatae, tuberculatae, valde costatae, rostratae. Pappi constati ex setis 100+, aequalibus, barbellatis, extimis deciduis. Pollina echinata. $2n = 18$.

Annual herbs. Leaf blades spatulate to oblong, deeply lobed to pinnatifid; margins white, scarious, dentate or setose-ciliate. Capitula borne singly or

capitulescences sparingly branched. Receptacles not paleate, not bristly. Involucres cylindrical to urceolate, at base with spatulate bracts with margins white, scarious, toothed. Phyllaries 2-seriate, \pm equal. Florets 7 to 16 per capitulum. Corollas cream-colored to light yellow (when dry, pink). Cypselae clavate, tuberculate, strongly ribbed, beaked. Pappi of 100+ equal, barbellate bristles, the outermost deciduous. Pollen echinate (Tomb et al., 1974). Chromosome number $2n = 18$.

Included genus: *Glyptopleura* D. C. Eaton.

Krigiinae Joongku Lee & B. G. Baldwin, subtribus nov. TYPE: *Krigia* Schreber.

Herbae annuae vel perennes. Laminae foliorum lineares, oblongae, lanceolatae, vel oblanceolatae; margines integri, lobati, vel pinnatifidi. Capitula portata singulatim vel capitulescentiae cymosae vel interdum superne subumbellatae. Receptacula epaleata. Involucra turbinata, campanulata, vel urceolata. Phyllaria 1–2+-seriata, aequalia. Flosculi 4–30. Corollae flavae vel aurantiacae. Cypselae columnares vel ovoideae, 10–20-nervatae vel -costatae, non rostratae. Pappi nulli vel ex squamis 5+ constati (interdum fascientibus coronis minutis), plerumque cingentibus setis 5+, inaequalibus, spiculatis. Pollina echinolophata. $2n = 8, 10, 12, 18, 20, 30$, vel 60.

Plants annual or perennial herbs. Leaf blades linear, oblong, lanceolate, or oblanceolate; margins entire, lobed, or pinnatifid. Capitula borne singly or capitulescences cymiform or subumbelliform. Receptacles not paleate. Involucres turbinate, campanulate, or urceolate. Phyllaries 1- or 2+-seriate, equal. Florets 4 to 30 per capitulum. Corollas yellow or orange. Cypselae columnar or ovoid, 10- to 20-nerved or -ribbed, not beaked. Pappi none or of 5+ scales (sometimes forming minute crowns), usually surrounding 5+, unequal, spiculate bristles. Pollen echinolophate (Feuer & Tomb, 1977). Chromosome number $2n = 8, 10, 12, 18, 20, 30$, or 60.

Included genus: *Krigia* Schreber.

Lygodesmiinae Joongku Lee & B. G. Baldwin, subtribus nov. TYPE: *Lygodesmia* D. Don.

Herbae annuae (*Shinnersoseride*) vel perennes. Laminae foliorum lineares vel lanceo-lineares (vel squamiformes distaliter); margines plerumque integri, interdum lobati. Capitula raro portata singulatim, capitulescentiae plerumque ramosissimae. Receptacula epaleata. Involucra cylindracea vel subcylindracea. Phyllaria 2-seriata, inaequalia (extimis fascientibus calyculis). Flosculi 5–12. Corollae subrosaceae, purpureae, vel albae. Cypselae columnares vel fusiformes, laeves, striatae, rugosae, vel costatae, non rostratae. Pappi ex setis 24–250, aequalis, barbellatis (et squamis 5, subulatis in *Chaetadelpha*), constati omnibus persistentibus. Pollina echinata vel echinolophata (*Lygodesmia*). $2n = 12$ (*Shinnersoseride*) vel 18, vel 27 (triploideis).

Annual (*Shinnersoseris*) or perennial herbs. Leaf blades linear or lance-linear (or scale-like distally); margins usually entire, sometimes lobed. Capitula rarely borne singly, capitulescences usually much-branched. Receptacles not paleate. Involucres cylindrical or subcylindrical. Phyllaries 2-seriate, unequal (the outer forming calyculi). Florets 5 to 12 per capitulum. Corollas pink, purple, or white. Cypselae columnar or fusiform, smooth, striate, rugose, or ribbed, not beaked. Pappi of 24 to 250 equal, barbellate bristles (and 5, subulate scales in *Chaetadelpha*), all persistent. Pollen echinate or echinolophate (*Lygodesmia*) (Tomb et al., 1974). Chromosome number $2n = 12$ (*Shinnersoseris*) or 18, or 27 (triploids).

Included genera: *Chaetadelpha* A. Gray, *Lygodesmia* D. Don (sensu Tomb), *Shinnersoseris* Tomb.

Phalacroseridinae Joongku Lee & B. G. Baldwin, subtribus nov. TYPE: *Phalacroseris* A. Gray.

Herbae perennes. Laminae foliorum lineares, lanceolines, vel oblanceolatae; margines integri. Capitula portata singulatim (pedunculis scapiformibus); receptacula epaleata; involucra campanulata; phyllaria 2+-seriata, aequalia. Flosculi 13+, corollae flavae. Cypselae fusiformes, laeves, non rostratae; pappi nulli. Pollina echinolophata. $2n = 18$.

Perennial herbs. Leaf blades linear, lance-linear, or oblanceolate; margins entire. Capitula borne singly (peduncles scapiform). Receptacles not paleate. Involucres campanulate. Phyllaries 2+-seriate, equal. Florets 13+ per capitulum. Corollas yellow. Cypselae fusiform, smooth, not beaked. Pappi none. Pollen echinolophate (Feuer & Tomb, 1977). Chromosome number $2n = 18$.

Included genus: *Phalacroseris* A. Gray.

Pinaropappinae Joongku Lee & B. G. Baldwin, subtribus nov. TYPE: *Pinaropappus* Lessing.

Herbae perennes vel frutices rosulatae (*Marshalljohnstonia*). Laminae foliorum lineares (vel squamiformes distaliter), ellipticae, vel rhombeae; margines integri, dentati, vel lobati. Capitula portata singulatim. Receptacula paleata (*Pinaropappo*) vel epaleata. Involucra obconica vel campanulata. Phyllaria 3+-seriata, inaequalia. Flosculi 10–18. Corollae subrosaceae, purpureae, vel albae. Cypselae sulcis 5, angustis, aequaliter dispositis, columnares vel fusiformes, non rostratae (distaliter attenuatae in *Pi-*

naropappo p.p.). Pappi ex setis 40–60, aequalis, barbellatis, persistentibus constati. Pollina echinata. $2n = 18$ vel 36.

Perennial herbs or rosette shrubs (*Marshalljohnstonia*). Leaf blades linear (or scale-like distally), elliptic, or rhombic; margins entire, dentate, or lobed. Capitula borne singly. Receptacles paleate (*Pinaropappus*) or not paleate. Involucres obconic or campanulate. Phyllaries 3+-seriate, unequal. Florets 10 to 18 per capitulum. Corollas pink, purple, or white. Cypselae columnar or fusiform, with 5 narrow, equally spaced furrows, not beaked (distally attenuate in *Pinaropappus* pro parte). Pappi of 40 to 60 equal, barbellate bristles, persistent. Pollen echinate (Tomb et al., 1974). Chromosome number $2n = 18$ or 36.

Included genera: *Marshalljohnstonia* Henrickson, *Pinaropappus* Lessing.

Pyrrhopappinae Joongku Lee & B. G. Baldwin, subtribus nov. TYPE: *Pyrrhopappus* DC.

Herbae annuae vel perennes. Laminae foliorum ellipticae, lanceolatae, vel oblanceolatae; margines integri vel pinnatifidi. Capitula portata singulatim vel capitulescentiae laxe corymbiformes. Involucra cylindracea vel anguste campanulata. Phyllaria 2-seriata, inaequalia (extimis fascientibus calyculis). Flosculi 30–150+. Corollae flavae, purpureae, vel albae. Cypselae fusiformes, 5–12-costatae, rostris fragilibus. Pappi ex setis 119–155, aequalis, barbellatis (cum pilis minutis, reflexis subtentis in *Pyrrhopappo*) constati, persistentibus. Pollina echinata (*Picrosia*) vel echinolophata (*Pyrrhopappo*). $2n = 12, 14$, vel 24.

Annual or perennial herbs. Leaf blades elliptic, lanceolate, or oblanceolate; margins entire or pinnatifid. Capitula borne singly or capitulescences loosely corymbiform. Receptacles not paleate. Involucres cylindrical to narrowly campanulate. Phyllaries 2-seriate, unequal (the outer forming calyculi). Florets 30 to 150+ per capitulum. Corollas yellow, purple, or white. Cypselae fusiform, 5- to 12-ribbed, beaks fragile. Pappi of 119 to 155 equal, barbellate bristles (subtended by minute, reflexed hairs in *Pyrrhopappus*), persistent. Pollen echinate (*Picrosia*) or echinolophate (*Pyrrhopappus*) (Feuer & Tomb, 1977). Chromosome number $2n = 12, 14$, or 24.

Included genera: *Picrosia* D. Don, *Pyrrhopappus* DC.

KEY TO PRINCIPALLY NORTH AMERICAN SUBTRIBES OF CICHORIEAE

- 1a. Capitulescences monocephalic (capitula borne singly); cypselae not ribbed or furrowed; pappi absent Phalacroseridinae
- 1b. Capitulescences corymbiform to thyrsoid-paniculiform or subumbelliform, or if monocephalic, then cypselae ribbed or furrowed and pappi present (rarely absent in *Microseris douglasii*).
 - 2a. Cypselae beaked.
 - 3a. Some or all pappus bristles caducous or fragile.

- 4a. Capitulescences stipitate-glandular (gland heads \pm disk-shaped); pappus bristles falling together Malacothricinae p.p. (*Calycoseris*)
- 4b. Capitulescences not stipitate-glandular; outer pappus bristles caducous or fragile, the inner persistent Glyptopleurinae
- 3b. Pappus bristles persistent.
 - 5a. Pappus bristles plumose Stephanomeriinae p.p. (*Rafinesquia*)
 - 5b. Pappus bristles barbellate or smooth.
 - 6a. Capitulescences monocephalic; corollas yellow or orange; beaks shorter than to much longer than bodies of cypselae; apices of beaks glabrous . . Microseridinae p.p. (*Agoseris*)
 - 6b. Capitulescences usually loosely corymbiform, sometimes monocephalic; corollas yellow, purple, or white; beaks much longer than bodies of cypselae; apices of beaks glabrous or villous (if capitulescences monocephalic and corollas yellow, then apices of beaks villous) Pyrrhopappinae
- 2b. Cypselae not beaked (apically attenuate in *Pinaropappus* and *Uropappus*).
 - 7a. Corollas usually yellow or orange (if white, then pappi of scales, scales and bristles, or bristle-tipped scales); pollen echinolophate.
 - 8a. Phyllaries in 1 or 2 series, subequal, the outer not forming calyculi; pappi of scales or scales and bristles Krigiinae
 - 8b. Phyllaries in 2+ series, subequal or unequal, the outer sometimes forming calyculi; pappi of bristle-tipped scales or bristles Microseridinae
 - 7b. Corollas often pink or purple (if yellow or white, then pappi absent (*Atrichoseris*) or of only bristles); pollen usually echinate (echinolophate in *Lygodesmia*).
 - 9a. Receptacles not paleate, often bristly; florets 15 to 250 per capitulum; corollas usually yellow, sometimes white; pappus bristles often all or mostly caducous or readily falling Malacothricinae
 - 9b. Receptacles usually not paleate, rarely paleate (*Pinaropappus*), not bristly; florets 3 to 18 per capitulum; corollas usually pink or purple, sometimes white; pappus bristles usually persistent.
 - 10a. Capitulescences monocephalic; phyllaries in 3+ series, unequal Pinaropappinae
 - 10b. Capitulescences usually corymbiform to thyrsoid-paniculiform, rarely monocephalic; phyllaries usually in 2 unequal series, the outer forming a calyculus.
 - 11a. Plants non-thorny herbaceous perennials or opposite-leaved annuals (*Shinnersoseris*); pappus bristles barbellate; pollen usually echinolophate, rarely echinate (*Chaetadelpha*, *Shinnersoseris*) Lygodesmiinae
 - 11b. Plants thorny and non-thorny herbaceous perennials, alternate-leaved annuals, or shrubs; pappus bristles usually plumose (if barbellate and plants herbaceous perennials, then stems thorny (*Pleiacanthus*)); pollen echinate Stephanomeriinae

An expanded phylogenetic study of Malcothri-
cinae is under way to resolve the memberships of
lineages within the non-monophyletic *Malacothrix*,
prior to generic redelimitation. We are also studying
relationships of *Thamnoseris* (endemic to Islas Des-
venturadas, Chile), which was included by Stebbins
(1953) in Stephanomeriinae. Data from additional
gene regions are needed to gain refined under-
standing of the relationships among the subtribes
of New World Cichorieae treated here.

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